TAPHONOMY AND ARCHAEOLOGICALLY RECOVERED MAMMAL BONE FROM SOUTHEAST MISSOURI

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ABSTRACT.—A number of nonhuman predators have been identified by zooarchaeologists and paleontologists as potentially contributing to, or otherwise affecting, the pre-depositional histories of faunal assemblages. Studies of modern bone destruction and modification resulting from feeding activities of gray wolves, and analysis of preferred prey species of owls are applied to identified mammal bone from Granite Quarry Cave in Southeast Missouri. Close similarity between mammal remains resulting from wolf and owl predation and archaeologically recovered remains from Granite Quarry Cave indicates that nonhuman agents were responsible for a large proportion of the archaeological faunal assemblage.

INTRODUCTION

A number of taphonomic agents have been identified by zooarchaeologists and paleontologists as potentially contributing to, or otherwise affecting, the pre-depositional histories of faunal assemblages (Andrews and Evans 1983; Blumenschine 1986; Brain 1981; Hill 1979; Levinson 1982; Potts 1984; Mayhew 1977). Recent studies of nonhuman bone accumulating and modifying agents in North America include, among others, activities of carnivorous predators such as wolves, coyotes, foxes, badgers, and cats, and raptors such as owls and hawks (e.g., Bickart 1984; Binford 1981; Bonnichsen 1973; Dodson and Wexlar 1979; Haynes 1982; Korth 1979; Kusmer 1986; Mellett 1974). Of these animals, two groups of predators, the canids (particularly wolves) and raptors (owls) are now, or have been in the relatively recent past, widespread across the North American continent (Bent 1938; Hall 1981).

Beginning in 1986 studies were conducted by the authors on bone modification by gray wolves (Snyder and Klippel 1986) and on preferred prey of owls inhabiting the southeastern United States (Klippel and Parmalee 1986). Recent identification and description (Klippel *et al.* 1986) of an archaeological vertebrate assemblage from Granite Quarry Cave (23CT36), located on the Current River in Southeast Missouri, provided an opportunity to apply information gathered through actualistic studies to the interpretation of an archaeologically recovered faunal assemblage.

THE ARCHAEOLOGICAL SITE

Granite Quarry Cave (23CT36) is a west-facing cave situated high on a limestone bluff along the left bank of the Current River in Carter County, Missouri. The cave entrance is approximately 9.5 m wide and 3.5 m high at the dripline, and the entrance passage extends roughly 30 m back into the bluff before opening into a larger room.

Archaeological testing by James Price in 1985 revealed culture-bearing deposits extending ca. 15 m from the dripline into the cave and to a maximum depth of approximately 60 cm below the surface (Price 1986). Three one-meter square test units, plus a portion of a fourth, were excavated and deposits screened through 6.4 mm (¼-inch) mesh hardware cloth. Price identified five strata within the cave deposits: predominately Historic, Mississippian, two underlying nonceramic zones and a basal stratum lacking cultural materials. Archaeological materials recovered during testing included 53 shell tempered sherds, 23 lithic artifacts, 2 modified bone artifacts, and 2 modified shell artifacts; debitage included ca. 2,500 chert flakes, 825 shells and shell fragments (the majority of which were from terrestrial species), and roughly 7,000 bones and bone fragments. Detailed descriptions of these materials are provided by Price (1986) and Klippel *et al.* (1986).

CANID FEEDING BEHAVIOR

Carnivorous predators may leave a residue of broken and scattered bone in a variety of settings such as kill sites, denning areas, or temporary resting and gathering spots (Binford 1981; Brain 1981; Sutcliffe 1970). When these areas are also the locus of human activities the resultant deposit will be a mixture reflecting both the human and nonhuman contributors. In order to recognize the contributions of nonhuman predators, it is necessary to isolate and characterize residues and damage patterns produced by the carnivores themselves.

In North America, the effects of wild predators on prey species have been studied by both wildlife biologists interested in predator prey relations (e.g., Floyd *et al.* 1979; Mech 1966, 1970; Pimlott *et al.* 1969) and by paleontologists and archaeologists interested in assessing the contributions of various taphonomic agents to bone accumulations (e.g., Mellett 1974; Haynes 1981, 1982, 1983).

Haynes, in particular, has studied a wide range of predators; he has collected information from kill sites, denning areas, and controlled feeding of zoo animals. Results of these studies have been influenced by both the varied activities of free ranging animals in the wild and by the artificial surroundings and feeding limitations often placed on zoo populations.

Control data.—Our study focusses on a single predator, the gray wolf *(Canis lupus)*, once common throughout much of North America (Hall 1981; Young and Goldman 1944), and a single prey species, the white-tailed deer *(Odocoileus virginianus)*, also common throughout much of eastern North America prehistorically. Circumstances of the study allowed the animals unrestricted access to "prey" carcasses, and controlled recovery of nearly all bone including remains from feeding activity and scatological materials.

In this study one adult female and four adult male wolves were allowed to range freely in a tree filled enclosure measuring approximately 38 m by 15 m. Three of the males were 3.5 year-old litter mates weighing between 45 and 50 kg. The fourth male was seven years old and weighed about 49 kg; the 2.5 year-old female weighed approximately 32 kg.

The wolves have been kept in this enclosure since April 1979, which contains an artificial den constructed of metal drainage pipes covered with earth and rocks. Since there is no ground cover, surface visibility is excellent. The usual diet of the wolves consists of commercially prepared dry dog food fed daily and one chicken per wolf, once a week. In addition, they are occasionally fed portions of deer or beef carcasses donated by local hunters and farmers.

Between March and November (1986) fresh, undressed carcasses of road-killed deer were placed within the enclosure at periodic intervals as they became available. Before a fresh carcass was introduced the entire pen area was surveyed, and all bone debris removed. While a carcass was being monitored the wolves received no other food.

Over the course of the study a consistent pattern of carcass reduction and disarticulation was observed. In the first 24 to 48 hours major meat sections such as the hindquarters were consumed, the thoracic cavity opened and ribs eaten away. The throat was also sometimes opened, and the nose was often eaten away. Within 48 hours disarticulation of one or more limbs occurred, usually forelimb before hind limb. Following consumption of meaty parts there was extensive destruction of limb bones, the vertebral column and associated rib heads and proximal shafts. In nearly all cases, remnants of the vertebral column and hide were the last carcass portions consumed. When all meat was consumed and the wolves showed no further interest in the remains (usually 4 to 7 days), the surface of the enclosure was surveyed and all remaining bone and bone fragments collected. Elements recovered from four deer carcasses are summarized in Table 1.

Of the skull and axial skeleton, tooth rows—both maxillary and mandibular—survived well, as did innominates. All left and right mandibles were represented, although the degree of destruction to individual elements varied. Seven of eight innominates also survived in identifiable form, most commonly the acetabula with broken ischial, pubic or ilial wings. Conversely, only one partially complete cranium was recovered, and vertebrae were poorly represented. Only three cervical vertebrae, exclusive of the atlases, and two of 52 thoracic vertebrae were recovered.

Of the appendicular skeletal units, the sturdiness of two joints, the distal humerus-proximal radius/ulna and distal tibia-proximal metatarsal, were exhibited in several instances in which these elements were found still firmly articulated and bound by dried bits of muscle and ligament. No distal radii or ulnae survived and only two of 48 carpals were collected. Many of the larger fibular tarsals and tibial tarsals, and seven of eight proximal metatarsals were recovered. Metacarpal and metatarsal shafts, still encased in hide, were also common. Finally, of 96 first, second, and third phalanges, only one was recovered.

In addition to remaining bone debris, wolf scats were collected throughout the period in which each carcass was consumed. During the initial 24-48 hour period, when primarily meat was being consumed, scats were very liquid and dark, and contained little or no bone. As bone and hide were eaten, scats became firmer, and hair and bone were often visible on their surfaces. Individual scats were cataloged and processed by water-screening through 1.6 mm (1/16 inch) mesh sieves to recover all bone fragments and hair. Some contained no observable bone or hair, others appeared to be composed primarily of tightly wrapped hair and little bone, and still others contained many identifiable and unidentifiable bone fragments. A total of 830 bone fragments larger than 6.4 mm (¼ inch) were recovered from a sample of 165 scats representing four deer carcasses; 260 of these specimens were identifiable to at least the element level.

The elements commonly occurring in scat (Table 2) reflect, to a large and perhaps predictable extent, those elements not present in recovered carcass debris. Carpals and the smaller tarsals made up approximately 6% of identified scat materials (Fig. 1, c,f).

TABLE 1. *Elements recovered from deer carcasses, 1986.*

Element	No. Expected	No. Observed	Percentage
Cranium	4	1	25.0
Mandible	8	8	100.0
Atlas	4	2	50.0
Axis	4	1	25.0
Cervical vertebra	20	3	15.0
Thoracic vertebra	52	2	3.8
Lumbar vertebra	24	7	29.2
Innominate	8	7	87.5
Rib	104	1	1.0
Scapula	8	4	50.0
Prox. humerus	8	2	25.0
Dist. humerus	8	7	87.5
Prox. radius/ulna	8	6	75.0
Dist. radius/ulna	8	0	0.0
Carpals	48	2	4.2
Prox. metacarpal	8	6	75.0
Dist. metacarpal	8	0	0.0
Prox. femur	8	2	25.0
Dist. femur	8	3	37.5
Prox. tibia	8	1	12.5
Dist. tibia	8	4	50.0
Tarsals	40	18	45.0
Fibular tarsal	8	4	50.0
Tibial tarsal	8	5	62.5
Prox. metatarsal	8	7	87.5
Dist. metatarsal	8	1	12.5
1st phalange	32	1	3.1
2nd phalange	32	0	0.0
3rd phalange	32	0	0.0

Number of elements expected based on four carcasses, observed equals elements recovered.

Twenty-five percent of identified elements were rib heads or shaft fragments, and 18.8% were vertebrae fragments. Distal metapodials, commonly missing from carcass debris, were represented in the scatological material by heavily pitted and eroded distal condyle fragments (Fig. 1, g). At least seven of 16 distal metapodials were identified in the scat materials. Phalanges (Fig. 1, h-i) and sesamoids made up 36.5% of identified bone from scats.

Alteration of bones due to consumption and erosion by digestive acids was also recorded. Three types of modification were observable macroscopically. Chunks of cancellous or compact tissue were often recovered, some of which still showed gnaw

TABLE 2. *Identifiable specimens recovered from wolf scats, 1986.*

Element	No. Identified	% Identified Material
Isolated teeth	2	0.8
Vertebrae fragment	49	18.8
Rib fragments	66	25.4
Costal cartilage	9	3.5
Forelimb	6	2.3
Carpals	10	3.8
Hind limb	5	1.9
Tarsals	6	2.3
Metapodials	12	4.6
1st phalange	6	2.3
2nd phalange	11	4.2
3rd phalange	11	4.2
Vestigial phalanges	32	12.3
Sesamoids	35	13.5

Percentages based on 260 identified specimens, representing four carcasses.

or puncture marks (Fig. 1, a-b). Additional puncture marks were probably masked by surface erosion of compact tissue. Many of these fragments have deer hair entangled in cancellous tissue, or firmly lodged in breaks and cavities (Fig. 1, b-c). A distinctive smoothing and rounded shallow pitting is common on compact bone surfaces. Some of these fragments show a high degree of polish or a sheen on their surfaces (Fig. 1, d-e). A number of specimens, particularly phalanges which are often swallowed whole, show eroding and thinning of compact bone tissue to the extent that the surface of the element is partially destroyed, and broken edges become nearly knife-edge thin (Fig. 1, h-i).

GRANITE QUARRY CAVE DEER REMAINS

Seventy-nine identifiable deer bones, representing at least four individuals, were recovered from test excavations within the cave (Table 3). Although no tooth-bearing elements suitable for ageing were recovered, 47 of the 79 elements (59.5%) were comparable in size to modern comparative skeletal materials from animals less than two weeks old and five to six months of age (Fig. 2). Wildlife studies have documented that wolves prey heavily on very young and very old ungulates, selecting the young particularly during the late spring and summer when they are most vulnerable. Thompson (1952:34-35) found remains of fawns in 45% of wolf scats, and remains of adult deer in 50% of scats collected during summer periods in Wisconsin. Sixty-one percent of scats collected in late summer contained remains of fawns, while only 31% contained adult deer remains, although he estimated the fawn to adult live population ratio to be approximately 1:3. Fawn hair occurred in 81% of wolf scats containing deer hair collected after May 31 in three years of study in Algonquin Park, Ontario (Voight *et al.* 1976:665), although the ratio of fawns to adults in the live population was assumed to be 1:1 or less. The high percentage (59.5%) of elements attributable to newborn or young of the year in the Granite

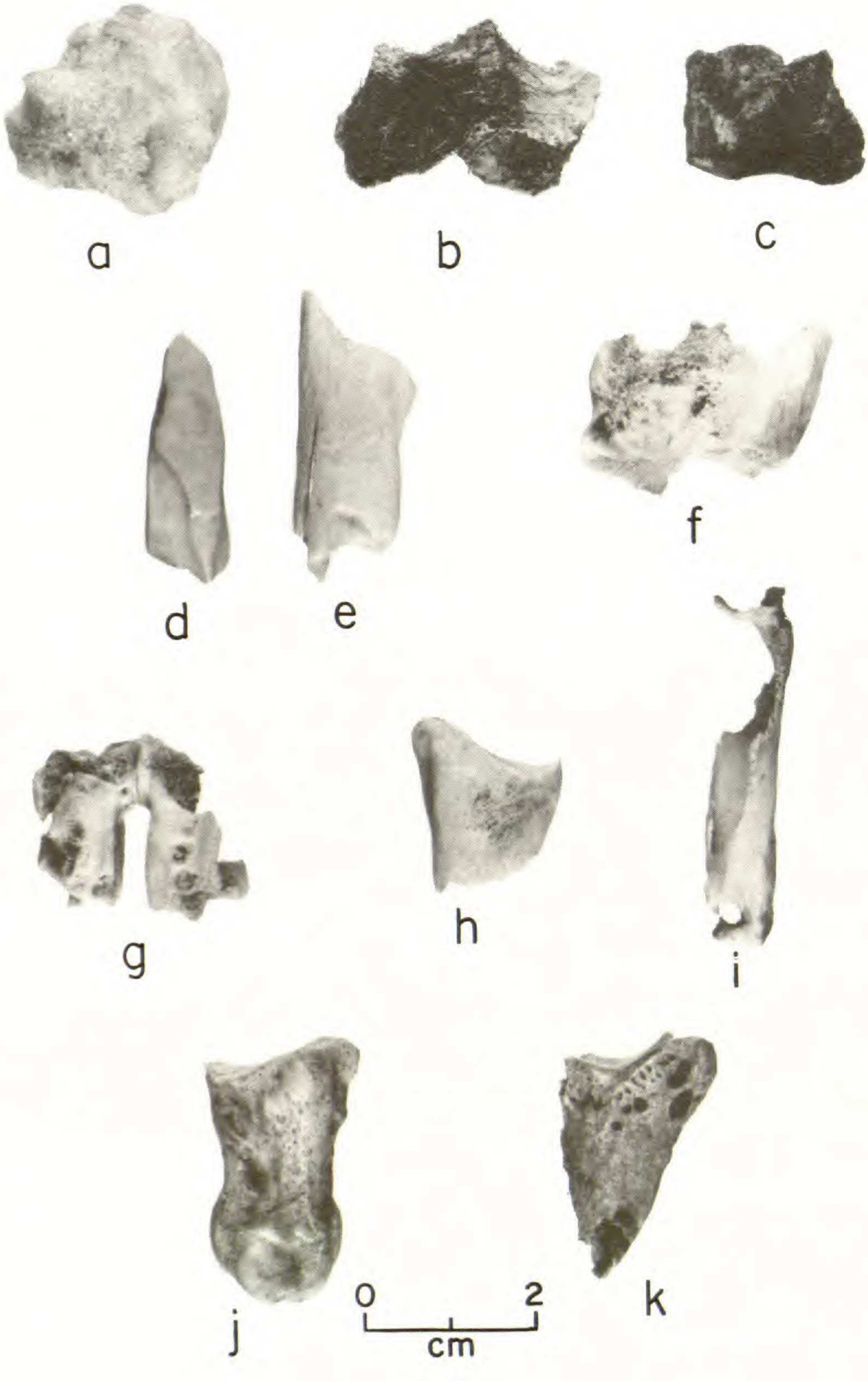

FIG. 1.—Partially digested deer bone from wolf scat (a-i) and deer elements (j,k) from Granite Quarry Cave.

TABLE 3. *Summary of identified mammal remains from the Granite Quarry Cave Site (23CT36), Carter County, Missouri.*

Taxa	Common Name	NISP	%NISP
Glaucomys volans	southern flying squirrel	1881	70
Insectivora	mole and shrew	269	10
Vespertilionidae	plainnose bat	160	6
Cricetidae	rat, mouse, vole, etc.	148	5
Odocoileus virginianus	white-tailed deer	79	3
Sciurus sp.	gray and/or fox squirrel	52	2
Geomys bursarius	plains pocket gopher	52	2
Procyon lotor	raccoon	13	<1
Sylvilagus floridanus	cottontail rabbit	13	<1
Marmota monax	woodchuck	7	<1
Tamias striatus	chipmunk	7	<1
Mephitis/Spilogale	striped & spotted skunk	7	<1
Didelphis marsupialis	opossum	4	<1
Canis sp.	wolf, coyote, dog	3	<1
Castor canadensis	beaver	1	<1
Vulpes/Urocyon	red or gray fox	1	<1
Felis concolor	puma	1	<1
Dasypus cf. *bellus*	giant armadillo	1	<1

Insectivora includes two species; Vespertilionidae, ≥five species; Cricetidae, ≥five species; other classes of vertebrates identified include: ≥seven species of fish; ≥fives species of amphibians; ≥13 species of reptiles; and ≥27 species of birds (Klippel, Snyder, and Parmalee 1986).

Quarry assemblage contrasts sharply with the sample from the nearby open Gooseneck Site (Smith 1975:28) in which no fawns were identified; 87.5% of the deer represented at the Gooseneck Site (based on MNI) fell within the 1-4 year age classes.

Based on element counts (NISP), the contrast in identified deer remains between the two sites is even more pronounced. Of 433 identified elements from Gooseneck, no fetal or neonatal specimens were noted and only 28 elements (6.5%) were judged to be those of juvenile or young adult animals (Mick 1982: Appendix C, 58-63).

Comparison of proportions of skeletal elements represented in the Granite Quarry assemblage with those recovered from wolf scats (Fig. 3) also suggests carnivores contributed to the archaeological assemblage. While frequencies of particular elements vary, it is notable that phalanges and sesamoids constitute 36.5% of the modern scat materials, 36.2% of young deer remains from Granite Quarry, and 32.1% of all Granite Quarry deer elements. Carpals and tarsals make up 6.0% of the Granite Quarry deer elements, and 6.1% of the modern scatological assemblage. Even more striking similarities between modern scat material and the Granite Quarry assemblage are evident in percentages of modification due to consumption and partial digestion by stomach acids. Clear evidence of pitting, thinning and erosion, and occasional gnaw marks occur on both adult deer elements (Fig. 1, j-k) and remains of very young animals (Fig. 2, b-c,f) from Granite Quarry Cave. Gnawing occurs on 6.0% of the Granite Quarry bone, 7.6%

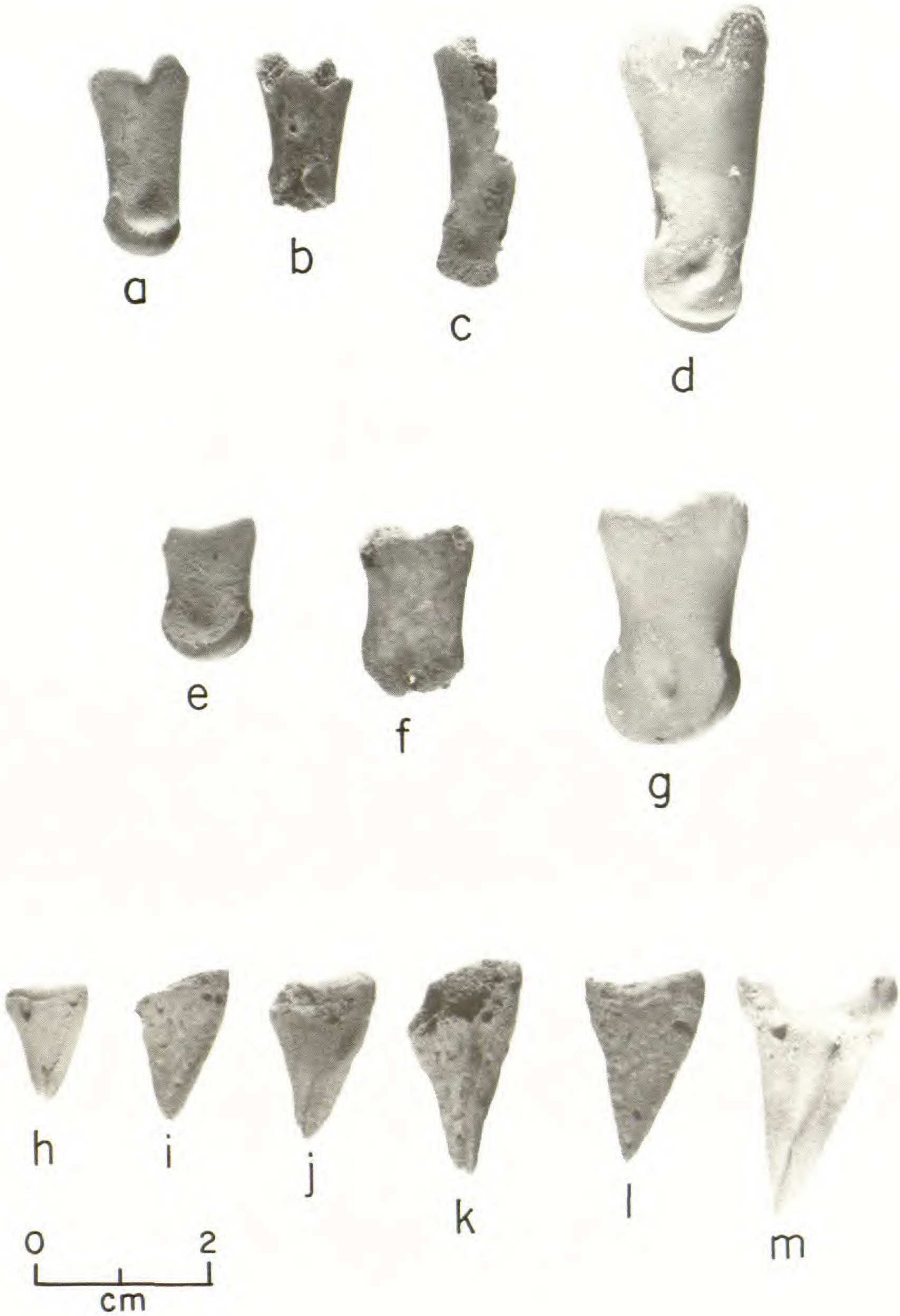

FIG. 2.—Deer phalanges from Granite Quarry Cave (b-c, f, i-l) and modern comparative specimens (UT Specimen No. 7238—0-2 weeks old: a,e,h; UT Specimen No. 7239—5-6 months old: d,g,m).

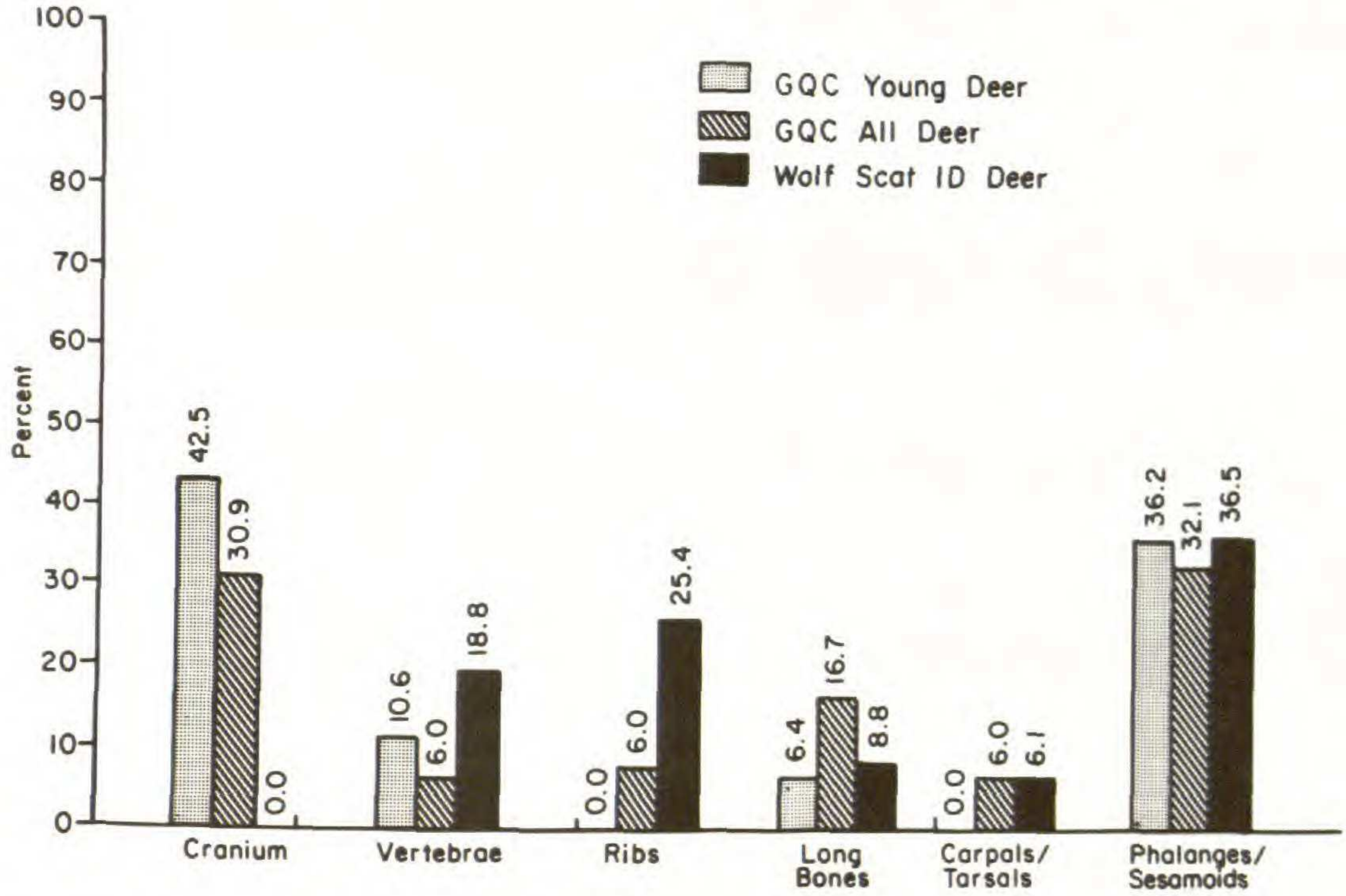

FIG. 3.—Identifiable deer remains from Granite Quarry Cave and modern deer elements from wolf scat.

of the modern scatological sample, and 4.2% of the identifiable bone from wolf scats (Fig. 4). Percentages of observed erosion and smoothing vary by less than 2% among the three defined groupings. Taken together, some form of observable alteration occurs on 32.1% of the Granite Quarry deer bone and 31.9% of the identifiable bone recovered from wolf scat.

The Granite Quarry deer bone assemblage is virtually identical to the scatological deer bone collected in the modern wolf study in degree of alteration due to consumption and erosion by digestive acids. This similarity, the high frequency of remains of very young animals, and the high relative percentages of phalanges and sesamoids in the Granite Quarry materials indicate that wild carnivores, perhaps wolves, probably were responsible for a substantial portion of the deer bone present in the cave deposit.

AVIAN PREDATION

Numerous bird species feed on other vertebrates; some consume and completely digest whole prey items while others regularly regurgitate undigested bone, hair, feathers, and scales. Raptors are known for their castings and among them owls tend to digest bone less than do hawks (Duke *et al.* 1975).

Some owl species regularly return to the same diurnal roost where subdued light is provided by coniferous trees, cavities in large trees, crevices in cliff or bluff faces, and in caves where irregularities in walls and ceilings provide potential roosts. The accumulation of reguritated owl pellets frequently produces a concentration of animal remains at such localities.

Control data.—In Middle Tennessee a wintering long-eared owl *(Asio otus)* returned to the same dead branch of a deciduous tree surrounded by the limbs of a red cedar *(Juniperus virginiana)* for three consecutive winters. During these periods the remains of an average

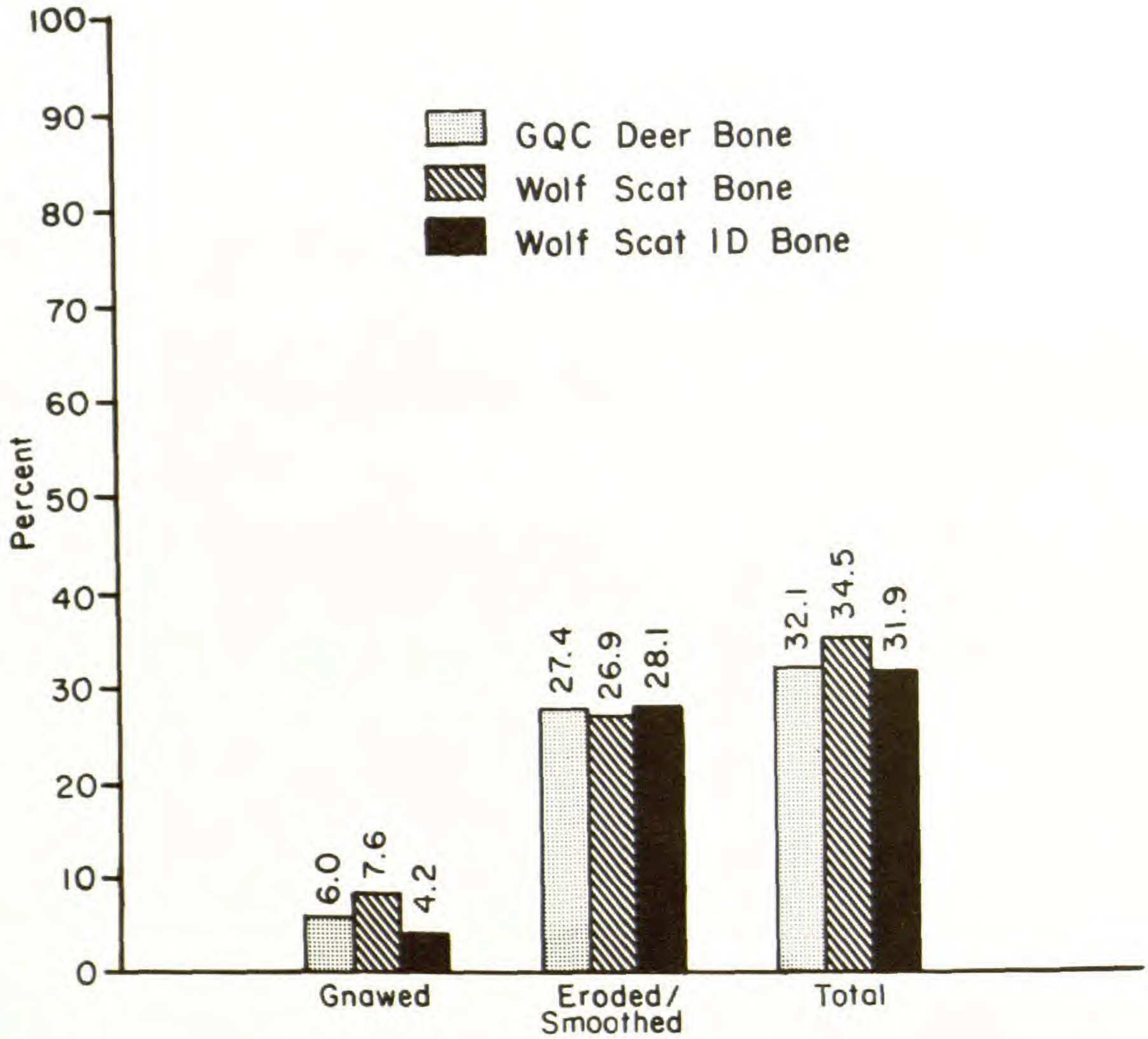

FIG. 4.—Observable alteration on Granite Quarry Cave deer remains and modern deer bone from wolf scat.

of 100 small mammals (MNI) accumulated each winter in an area of less than one square meter beneath the roost (Klippel and Parmalee 1982). Randle and Austing (1952:423) reported communal roosting of as many as 27 wintering long-eared owls in "a clump of four fifteen-foot pines" in southwestern Ohio. Hall and Blewett (1964:303) reported owl pellets and "a profusion of skeletal elements" accumulated by unidentified owls at the entrance of a cave in southern Missouri.

Studies of owl pellet contents have resulted in an extensive literature dealing with food preferences of various owl species inhabiting eastern North America. We have combined the results of our own owl pellet analyses with some of those in the literature for owls from eastern North America to develop estimates of prey size groups taken by six species of owls (*Bubo virginianus*, great horned owl; *Strix varia*, barred owl; *Tyto alba*, barn owl; *Otus asio*, screech owl; *Asio otus*, long-eared owl; and *Asio flammeus*, short-eared owl). All six inhabit large portions of the southeastern United States, at least seasonally, and all except *A. otus* and *A. flammeus* are year-round residents in the Southeast.

Because owls generally prey more heavily on mammals than they do on animals of other classes and because mammal remains are more frequently identified to the level of genus or species than are representatives of other classes of vertebrates, we have restricted our consideration of owl prey size to that of mammals. Sixteen sources were consulted to obtain information on over 40,000 prey items for the six species of owls (Eaton 1934; Errington 1932; Errington *et al.* 1940; Huber 1960; Klippel and Parmalee 1982; Korschgen and Stuart 1972; Latham 1950; Mendall 1944; Pearson and Pearson 1947; Randle and Austing 1952; Richmond and Roslund 1949; Rusling 1951; Stupka 1931; Terres and Jameson 1943; and Wilson 1938). Sources that described fewer than 100 prey items were excluded.

Median adult weights for reported prey taxa were obtained from ranges provided by Schwartz and Schwartz (1981). It was necessary to defer to Burt and Grossenheider (1964) for median weights of three taxa *(Tamiasciurus hudsonicus, Glaucomys sabrinus,* and *Lepus americanus)* that do not occur in Missouri. Prey taxa were subsequently assigned to one of four arbitrary weight categories (0-100 g; 100-1,000 g; 1,000-2,000 g; and >2,000 g).

When relative frequencies were calculated by weight categories, over 90% of the mammal prey taken by five of the six owl species fell into the 0-100 g range (Fig. 5). The single predator species that deviated from this pattern was the great horned owl; the weight of over 60% of their prey exceeded 100 g. Ninety-nine percent of the mammals weighing between one and two kg in the great horned owl diet were lagomorphs (rabbits and hares). However, if lagomorphs are excluded from the great horned owl prey taxa, their predation pattern is similar to the other five widespread southeastern owl species in that nearly 90% of the prey they take, exclusive of lagomorphs, weigh less than 100 g (Fig. 5).

GRANITE QUARRY MAMMAL REMAINS

In addition to 79 white-tailed deer elements discussed above, 2,620 mammal elements representing 29 taxa were identified from the Granite Quarry Cave faunal assemblage (Table 3). Over 85% of the elements (NISP) identified were those of individuals weighing less than 100 g. When remains were grouped into the four size categories described above and relative percentages calculated, the resulting profile is strikingly similar to that generated for five of the six species of owls (except the great horned owl) that regularly inhabit southern Missouri (Fig. 5). Potential roosts for owls within the cave, in the form of "solution pockets and overhangs" on the walls (Price 1986), along with the small size of the mammals represented in the Granite Quarry sample, strongly suggests the preponderance of small mammalian faunal remains were probably accumulated by raptors.

The species composition of mammals within the 0-100 g range is further suggestive of noctural raptor predation in that over 75% of the elements in this weight category are those of the southern flying squirrel *(Glaucomys volans).* According to Schwartz and Schwartz (1981), *G. volans* is totally nocturnal; as a result they would have been especially susceptible to predation by owls. Errington *et al.* (1940:791) and Mendall (1944:205) have both noted relatively high incidences of flying squirrels taken by the barred owl. This owl tends to favor hunting in forested habitats (an essential component of flying squirrel habitat) and is one of the year-round residents of southern Missouri. Roughly 30% of the flying squirrel remains from Granite Quarry Cave were recovered from deposits that generally postdate prehistoric human occupation at the site, further indicating use by a nonhuman predator such as the barred owl.

Faunal assemblages have been identified from two other nearby sites along the Current River. Deposits from Limekiln Cave (23SH109) were screened through 6.4 mm mesh and artifacts representing Mississippian and Woodland components were recovered (Lynott and Monk 1985). A variety of screening techniques were employed at the open, Mississippian Period, Gooseneck site (23CT34), but Mick (1982) reported the larger than

6.4 mm fraction faunal remains separately from those recovered with smaller screen mesh. The same screen mesh of 6.4 mm used at both Limekiln and Gooseneck as well as at Granite Quarry has afforded us the opportunity to compare the faunal remains.

Identified elements from Limekiln, Gooseneck, and Granite Quarry have been grouped according to the same four size categories (Fig. 5). Although recovery techniques were the same for the three assemblages, the remains are strikingly different. Far greater frequencies of elements representing taxa over 2 kg were recovered from both Limekiln Cave (>55%) and the Gooseneck site (>90%) than from Granite Quarry Cave (<10%).

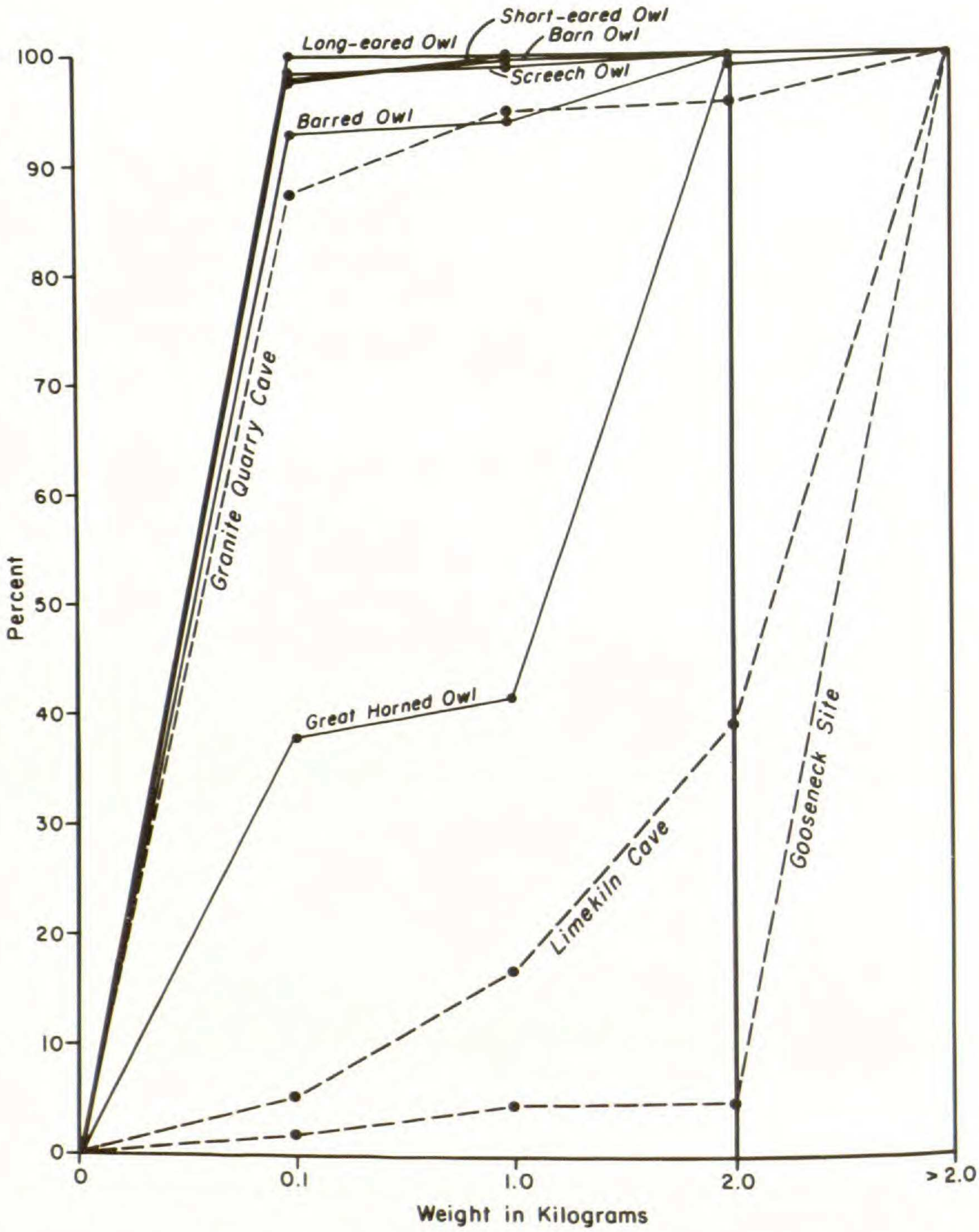

FIG. 5.—Size frequencies of mammals taken by great horned (n = 8,090), barred (n = 2,905), barn (n = 16,979), long-eared (n = 9,919), short-eared (n = 458), and screech owls (n = 1,997) compared to mammals (NISP) identified from Granite Quarry Cave (n = 2,699), Limekiln Cave (n = 105) and the Gooseneck Site (n = 416).

SUMMARY

Data collected in the modern wolf study indicate that certain skeletal elements are regularly consumed by wolves, and might be expected to accumulate in an area repeatedly used by these animals. Specific kinds of surface modification due to consumption and partial digestion are also documented. While this information does not provide a formula for assessing the degree of predator contributions to the Granite Quarry archaeological deer assemblage, the presence of these attributes, in proportions similar to those in the comparative sample from penned wolves, indicates a strong likelihood that a specific nonhuman agent has most likely affected this portion of the archaeological assemblage.

The majority of other mammal remains are also likely to have been introduced into Granite Quarry Cave deposits as a result of nonhuman activities. It has been well documented that some nocturnal raptors tend to haunt favored localities with subdued light, such as the twilight zones in caves, and that they are capable of accumulating large quantities of vertebrate remains in relatively short periods of time. It has also been demonstrated that these raptors generally prey on mammals of a fairly restricted size range (i.e. <2 kg) and that the majority of the remains in some archeologically recovered faunal assemblages (e.g. Granite Quarry Cave) fall well within this range.

Notwithstanding arguments that point out the high biomass afforded by small mammals and their potential as food items in prehistoric human diets (e.g. Stahl 1982), it is suggested here that predators other than humans are potential contributors to faunal assemblages recovered from many archaeological contexts. The context, composition, and condition of the Granite Quarry Cave faunal assemblage clearly indicate substantial contributions by nonhuman agents.

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